

***Guamampa* n.g. (Gastropoda, Pulmonata), a bradybaenid land snail with monadeniid characters**

by Anatoly A. SCHILEYKO

Abstract. — *Guamampa* n.g. is a genus of Aegistinae (Bradybaenidae) characterized by the presence of a single mucus gland entering the stylophore; the distal portion of vas deferens much enlarged; a flagellum of peculiar appearance; the penial verge grooved; and the vagina enlarged and coated with dense white cover. The type species is *Helix tuba* Albers, 1854 from Sulawesi, Indonesia. Certain characters of *Guamampa* and of *Tricheudota*, from the Philippines, are shared by the American genus *Monadenia*. Monadeniinae is elevated to family rank within the Xanthonychoidea.

Key-words. — Gastropoda, Pulmonata, Xanthonychoidea, Monadeniidae, *Guamampa*, Indonesia, systematics.

***Guamampa* n.g. (Gastropoda, Pulmonata), un Bradybaenidae avec des caractères de Monadeniidae**

Résumé. — *Guamampa* n.g. est un nouveau genre de Bradybaenidae Aegistinae défini par un ensemble de caractères de l'appareil génital : une seule glande muqueuse implantée sur le sac du dard ; la partie distale du vas deferens très développée ; un flagelle d'un type particulier, ressemblant à un poing ; la verge pénienne ouverte, présentant un profond sillon ; le vagin grand, couvert d'une enveloppe externe résistante. L'espèce-type est *Helix tuba* Albers, 1854, de Sulawesi (= Célèbes) en Indonésie. *Guamampa* et *Tricheudota*, des Philippines, partagent un certain nombre de caractères anatomiques avec le genre Nord-américain *Monadenia*. Le taxon Monadeniinae est élevé au rang de famille à l'intérieur de la superfamille Xanthonychoidea.

Mots-clés. — Gastéropodes, Pulmonés, Xanthonychoidea, Monadeniidae, *Guamampa*, Indonésie, systématique.

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INTRODUCTION

The problem of relationships of Eurasian and American helicoid land molluscs has been the subject of number recent discussions (MILLER & NARANJO-GARCIA 1989, 1991; NORDSIECK 1987; SCHILEYKO 1991). The author united Asian Bradybaenidae and American Xanthonychidae under a superfamily Xanthonychoidea (SCHILEYKO 1991). In this group, the condition of the sexual apparatus found in the subfamily Aegistinae is viewed as plesiomorphic when compared with that found in the Bradybaeninae, on one hand, and to Xanthonychinae (Xanthonychidae), on the other hand (SCHILEYKO 1991: 196, fig. 5). The condition observed in the subfamily Monadeniinae, from northwest America, is thus seen as immediately derived from the condition in Xanthonychinae. Conversely, MILLER & NARANJO-GARCIA (1989, 1991) include Monadeniinae

directly into the Asian Bradybaenidae. In this connection, it should be mentioned that more than 100 years ago PILSBRY (1894) pointed out the similarity of the mucus glands of the bradybaenid *Tricheulota*, from the Philippines, and of the American *Monadenia*.

In April 1995 I had an opportunity to dissect the species originally described as *Helix tuba* Albers, 1854 from Sulawesi (= Celebes), Indonesia. Peculiar features in the organisation of the reproductive apparatus lead me to establish a new genus for this species, and to discuss its systematic position and possible phylogenetic relationships.

ABBREVIATIONS

ag	albumen gland;	r	penal retractor muscle;
e	epiphallus;	s	stylophore;
f	flagellum;	st	spermatheca;
mg	mucus gland;	v	vagina;
p	penis;	vd	vas deferens;
pr	prostate;	vd1	slender proximal part of vas deferens;
ps	penis sheath;	vd2	distal part of vas deferens;
		ve	verge.

Family BRADYBAENIDAE Pilsbry, 1939
Subfamily AEGISTINAE Kuroda & Habe, 1949
GUAMAMPA n.g.

TYPE SPECIES. — *Helix tuba* Albers, 1854.

MATERIAL EXAMINED. — About fifteen specimens (four dissected) from limestone outcrop named Gua Mampu, near Uloe (Kampung Luppang, Desa Cabbeng), 30 km NNE of Watampone, South-West Sulawesi; altitude c.50 m. Collected by P. Bouchei, MNHN, 10 September 1991, under leaves of aroids.

ETYMOLOGY. — This genus is named after the locality where the present material was collected.

DESCRIPTION (Fig. 1)

Shell helicoid, depressed, rather thin but solid, somewhat translucent, of about 4.5 whorls; last whorl evenly rounded at periphery and slightly descending in front. Basic colouration consisting of yellow background with two brown or reddish bands above and below periphery; umbilicus encircled by area of same dark colour; in addition, two ill-defined bands, darker than background, one between adapical band and suture, the other between abapical band and circumumbilical area. Band width varies from reduced to hypertrophied. Initial part (0.3-0.4 whorl) of embryonic whorls smooth and polished, subsequently regularly radially wrinkled. Postnuclear surface nearly smooth, densely covered with very short golden hairs arranged in oblique series. Aperture wide, with broadly expanded and reflected whitish or pinkish lip. Umbilicus open, rather narrow. Height 17-20 mm, diameter 30-36 mm.

Talon, a small vesicle on a long slender duct, lying on surface of albumen gland. Vas deferens consisting of two parts: a long slender duct arising from prostate and an enlarged club-shaped portion entering epiphallus apically. Boundary between vas deferens and epiphallus marked by

flagellum of peculiar appearance, somewhat resembling a human fist with extended forefinger. Flagellum containing internally a series of narrow cavities entering the principal lumen of the duct at right angle, or nearly so. Epiphallus cylindrical, penial retractor attached to its middle portion. Apical part of the penis more or less bulbous, containing a verge in form of longitudinally folded fleshy plate, *i.e.* it is not closed, but grooved. Inner surface of distal part of penial tube covered by rows of prismatic tubercles. Stylophore voluminous, the only tubercular-alveolar mucus gland entering its lower part via thin duct; accessory sac absent. Vagina enlarged, with white dense external layer and thick walls filled with loose fibrous tissue. Spermathecal duct nearly cylindrical, spermathecal head lying *in situ* on surface of spermooviduct.

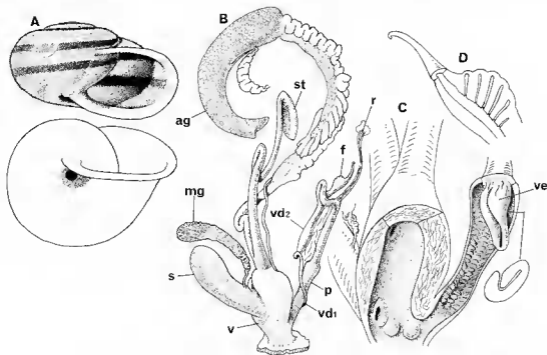


FIG. 1. — *Guamampa tuba*, Gua Mampu, SW Sulawesi, North of Bone (Matapone), P. Bouchet coll., september 1991. A, shell (actual size: height 18,7 mm, diameter 34,4 mm, 4,5 whorls). B, sexual apparatus. C, vagina and penis opened. D, longitudinal section of flagellum.

DISCUSSION

Besides the type species, *Guamampa* probably also include the following nominal species, as described and illustrated by SARASIN & SARASIN (1899): *Helix zonalis* Férussac, 1821; *H. exceptinucula* Beck, 1837, *H. expansa* L. Pfeiffer, 1861, *H. halmaherica* Kobelt, 1892, and *H. surrecta* Kobelt, 1894. All of these, and *H. tuba*, are usually placed in *Planispira* (Camaenidae), see *e.g.* RICHARDSON (1985). However, the occurrence of a stylophore, in association with other morphological genital characters, clearly excludes *Guamampa* from the

Camaenidae and allows its inclusion in the Bradydaenidae. In this family the subfamilies Aegistinae and Bradybaeninae differ by the presence (Aegistinae) or absence (Bradybaeninae) of the flagellum and by the occurrence in the Aegistinae of a small, but closed, tubular verge in the penis. The unusual structure of the flagellum described above and the latter character clearly connects *Guamampa* to the Aegistinae, a subfamily with taxa distributed throughout southern Asia including China, Japan, the Philippines and Indonesia.

From my dissections of *Aegista subchinensis* (Moellendorff, 1884), which is obviously very close to *A. chinensis* (Philippi, 1845), the type species of *Aegista*, the unusual structure of the flagellum described above in *Guamampa* is shared with *Aegista*. However other genital characters allow distinction between the two genera (Figs 2D, 3).

Genital morphology in *Guamampa* also resembles that observed in *Tricheulota* Pilsbry, 1895, type species (OD) *Chloritis spinosissima* Semper, 1880. The history of the type species is a little complicated. SEMPER (1873, pl. 14, figs 9a-b) first illustrated the reproductive anatomy of a species identified by him as *Helix sanziana* Hombrohn & Jacquinot, 1841. Later (SEMPER 1874, pl. 9, fig. 10) he published an illustration of a shell identified as *Helix sanziana* var. When the relevant text, with reference to the two aforementioned illustrations, was issued much later (SEMPER 1880: 235), Semper had changed the identification to *Chloritis spinosissima* n.sp. Whatever the real identity of the type species is, this would not change the present discussion because *Helix sanziana* and *Tricheulota spinosissima* are congeneric and most probably closely related. Conchological and genital characters are very similar in *Guamampa* and *Tricheulota* (Fig. 2A, B), but the flagellum exhibits the usual conical shape and the enlarged portion of the vas deferens is very short in *Tricheulota*, judging from SEMPER's illustration. (In addition, SEMPER did not show a penial retractor but this was probably not intentional).

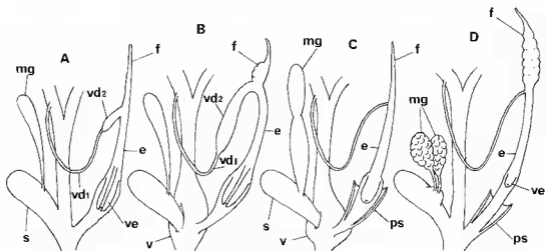


FIG. 2 — Distal parts of genitalia of four genera, schematized. A, *Tricheulota*. B, *Guamampa*. C, *Monadenia*. D, *Aegista*.

These aegistine genera can be compared to *Monadenia*, the type genus of the subfamily Monadeniinae which belongs to the family Xanthonychidae (Figs 2C, 4). *Monadenia* occurs in northwestern North America, roughly from Alaska to northern California (PILSBRY 1939). I have had the opportunity to dissect *M. infumata* (Gould, 1855) (material from Point Reyes National Seashore Park, Marin Co., California, 19 April 1989, coll. W. B. Miller) and *M. (Shastelix) troglodytes* Hanna & Smith, 1933 (material from Shasta Co., California, 16 August 1969, coll. B. Roth). Genital morphology in these species did not differ significantly from that in published illustrations of *M. fidelis* (Gray, 1834), the type species of the genus (e.g. PILSBRY 1939). *Monadenia* exhibits a mosaic of characters and/or character states shared with *Aegista*, *Tricheulota* and *Guamampa* :

- penial sheath and closed verge as in *Aegista*;
- a single club-shaped mucus gland as in *Tricheulota* and *Guamampa*;
- a simple conical flagellum like in *Tricheulota*.

However each taxon shows characters not shared with others:

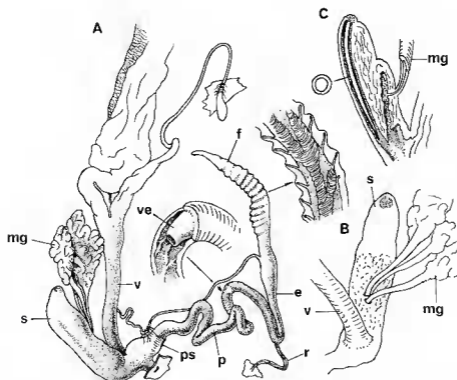


FIG. 3. — *Aegista subclunensis*, Taiwan, SW of Yeh-lu, Taipei Co., C.C. Coney coll., May 14, 1988. A, sexual apparatus (albumen gland omitted). B, stylophore from the other side. C, longitudinal section of stylophore.

- no penial sheath, grooved verge and enlarged distal region of the vas deferens in *Guamampa* and *Tricheulota*,
- occurrence of several mucous glands exhibiting a globular shape and alveolar structure in *Aegista*;
- mucous gland internally lamellar (Fig. 4) and clearly divided into gland proper and muscular duct in *Monadenia*.

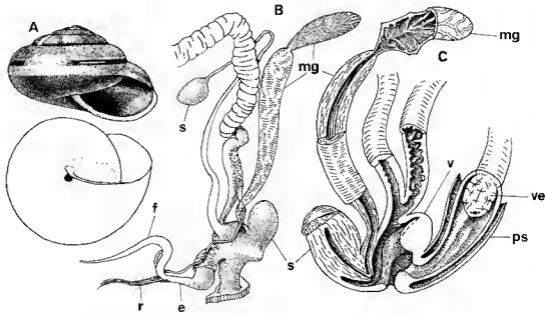


FIG. 4. — *Monadenia fidehs*, Middle Sisters Rock, Oregon, Field Museum of Natural History, Chicago, April 27, 1960. A, shell. B, sexual apparatus (albumen gland omitted). C, distal parts opened.

Guamampa has a single gland with alveolar structure as in *Aegista*, but this gland opens into a single duct as in *Monadenia*, although the duct is very short, slender and hardly muscularized. This duct could represent the first step of a morphocline leading to the condition observed in *Monadenia*, which would imply that the heavily muscular duct observed in *Monadenia* is derived from the basal region of the gland, irrespective of its initial structure. The unusual and complex structure of the lower vagina and atrium observed in *Monadenia* could also easily be derived from, or lead to, the very thick wall and thick external envelope of the homologous regions in *Guamampa*.

By comparison with other helicoid taxa, I propose the following conditions as plesiomorphic / apomorphic in the group of taxa discussed above:

- 1a. Occurrence of paired mucus glands with alveolar structure, opening into the accessory sac in (*Aegista*) / 1b. Reduction of one mucous gland associated with differentiation of the other

into a basal duct and an upper tubular glandular portion (*Tricheulota*, *Guamampa* and still more in *Monadenia*);

2a. Accessory sac well developed (*Aegista*) / 2b. Reduction of the accessory sac (all other genera discussed above);

3a. Penial verge grooved (*Tricheulota* and *Guamampa*) / 3b. Penial verge closed (tubular) (*Aegista* and *Monadenia*);

4a. Penial sheath present (*Aegista* and *Monadenia*) / 4b. Penial sheath reduced (*Tricheulota* and *Guamampa*);

5a. Flagellum simple, tapering (*Tricheulota* and *Monadenia*) / 5b. Complex structure of flagellum described above (*Aegista* and *Guamampa*);

6a. Vas deferens slender, evenly cylindrical (in *Monadenia* and *Aegista*) / 6b. Vas deferens differentiated into two regions (*Tricheulota* and *Guamampa*);

7a. Walls of the adatrial region with simple structure (*Aegista* and *Tricheulota*) / 7b. Walls of adatrial region thickened and complex in structure (*Guamampa* and still more in *Monadenia*).

When submitted to a procedure of parsimony (Hennig86), this data set resolves monophyly of *Tricheulota* and *Guamampa* (penial sheath reduced and distal vas deferens differentiated), but does not allow resolution of the trichotomy formed by this group, *Monadenia* and *Aegista*. However, similarities and mosaic pattern of character states shown and discussed above suggest close relationships of the Bradybaenidae (*Guamampa*, *Tricheulota*, *Aegista*) and Xanthonychidae (*Monadenia*). This interpretation is reinforced by the occurrence in some North American xanthonychid taxa (*Xanthonyx*, *Metostracon*, *Trichodiscina*, *Miraverellia*) of a pair of mucus gland similar to those observed in *Aegista*. However, in these taxa the glands are not alveolar but exhibit internal anastomosing folds as in *Monadenia*. In consequence, I propose to include the Bradybaenidae in the Xanthonychoidea to which *Monadenia* belongs. As we have come to the conclusion that *Monadenia* was derived independently from ancestors other than those of the rest of american helicoids, its taxonomic rank should be elevated up to family (Monadeniidae). Further investigation should allow reanalysis of this vast set of taxa, and in particular allow exploration of the various biogeographical interpretations of the apparent vicariance of the Bradybaenidae and Xanthonychidae on each side of the Behring strait.

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